THE ANATOMY OF CHEILANTHES VELLEA.

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(Twenty Text-figures.)
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Introduction.

In a previous paper (Bot. Gaz. lxxviii, No. 4, 1924), the writer described the anatomy of *Cheilanthes tenuifolia*. The interest of this type lies in the fact that the rhizome possesses a true dictyostelic structure, while the petiolar stele consists of a single strand. The xylem elements of the latter contain three protoxylem groups, the median one of which varies in position until it finally becomes exarch in position and then completely detached from the metaxylem elements. Since there is so much variation of stem and petiolar anatomy in the various species of the genus *Cheilanthes*, the investigation of *Ch. vellea* (one of the other two species common in New South Wales) was undertaken for the purpose of comparison with *Ch. tenuifolia* and other foreign types.

Marsh (1914) described four American species namely *Ch. persica*, *Ch. fendleri*, *Ch. gracillima* and *Ch. lanuginosa*. Gwynne-Vaughan (1903) described the stelar anatomy of *Ch. lendigera* and *Ch. microphylla*. All these types show considerable divergence of stelar structure, but, at the same time, form an excellent series for studying the gradual transition from solenostely to dictyostely. Prantl (1882) described the development of the young sporangia of *Cheilanthes* and considered that as the young sporangia develop quicker than the margin, the appearance is almost as though they sprang directly from the marginal cells.

The various species of the genus *Cheilanthes* are mostly small ferns with short horizontal rhizomes. This is the case in *Ch. vellea*: the external morphology shows various adaptations to the xerophytic habitats. The fronds are stiff and pinnately compound: the lower side is often brownish and always covered with a dense growth of hairs. The pinnae are usually opposite, in *Ch. tenuifolia* they are alternate. The sori are continuous and protected by the inrolled margin of the leaf. *Ch. vellea* is common in the dry parts of the interior of New South Wales.

The material for the present investigation was collected at Wiseman's Ferry (1923) and at Pennant Hills (1926). The material was fixed in a 1% chromo-acetic solution, washed, dehydrated and passed in the usual manner into paraffin. Sections were then cut 5 μ to 12 μ in thickness: Flemming's Triple stain, also Safranin and Haematoxylin were the staining processes most extensively employed.

The anatomy of *Ch. vellea* very closely resembles that of *Ch. tenuifolia* with various differences principally in the stelar structure of the petiole.

Investigation.

A. *Rhizome.*

The rhizome is covered by a fairly extensive development of scales, which are very dense around the apex. As indicated in Text-fig. 1, the apex is broad and flat, while the apical cell arises as a small conical emergence. The apical cell is tetrahedral in shape and segmentation is identical with that described in *Ch. tenuifolia* (1924). About 1mm. behind the apex, the whole of the ground tissue becomes sclerized.

In *Ch. vellea* the structure of the stem stele is of that type known as the dictyostele, due to the overlapping of the leaf gaps (Text-fig. 2). Although the
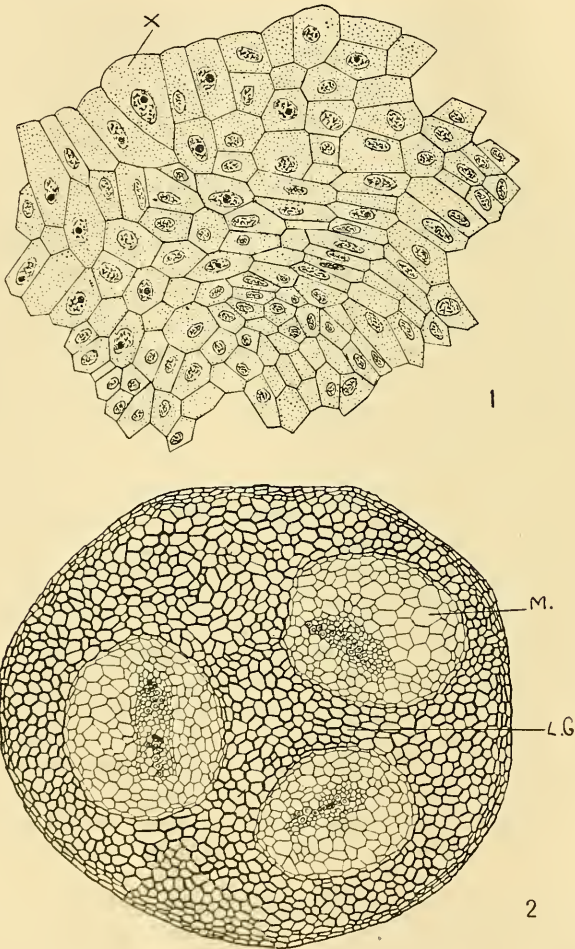
Text-fig. 1. Longitudinal section of the apex of the rhizome. The apical cell (X) is tetrahedral in shape and forms the typical segments. × 240.

Text-fig. 2. Transverse section of the rhizome indicating its dictyostelic structure. Three meristeles (M) are shown and three overlapping leaf gaps (L.G.). × 60.

structure is dictyostelic, it is only a simple type of such a form of anatomy as there were never more than three or four leaf gaps present in any section examined. *Ch. tenuifolia* is a more advanced type in this respect as the vascular cylinder is more frequently broken by leaf gaps than in *Ch. vellea*. The stelar anatomy of these two types at once places them near *Ch. persica* (Marsh, 1914) which is also a distinctly dictyostelic form. The other types which have so far been investigated show considerable variation of stelar structure.

Ch. fendleri (Marsh, 1914) is a true solenostele.

In *Ch. gracillima* (Marsh, 1914), the stele behaves as a true solenostele except at certain points where apparently two leaves are given off together.

In *Ch. lendigera* and *Ch. microphylla* (Gwynne-Vaughan, 1903), each leaf gap in the stele is closed before the next above is formed, so far as the endodermis and pericycle are concerned. The leaf-gap in the xylem, however, remains open until it overlaps with the gap formed in the xylem by the departure of the next leaf-trace above.

In *Ch. lanuginosa* (Marsh, 1914), the leaf traces are given off singly, in pairs or even in threes, so that at intervals the vascular cylinder may be a complete ring, though more frequently it is broken giving a dictyostelic structure (*cf.* Marsh, Text-fig. 14).

This series taken in conjunction with *Ch. vellea, Ch. persica* and *Ch. tenuifolia* indicate well a gradual transition from solenostely to dictyostely.

In *Ch. vellea*, as in all the other types, the leaf trace comes off from the centre of the meristele; its separation from the stem stele is not effected synchronously on both sides. The root trace passes off in the usual manner.

As indicated in Text-fig. 3, the meristele is composed of a central core of xylem intermingled with which is a little xylem-parenchyma. There is no trace of protoxylem present in the rhizome, even at the apex, all the tracheids of the xylem having sclariform thickening on their walls. The central core of xylem is not as wide as that present in *Ch. tenuifolia*, nor is there so much xylem parenchyma present. This is precisely the condition which follows on Marsh's generalization, since *Ch. tenuifolia* has a more complicated dictyostele than that present in *Ch. vellea*. Marsh (1914) found that there is a close relation between the stelar structure and the amount and arrangement of the wood within the stele. In solenostelic types there is a narrow continuous band of tracheids, not broken up by parenchyma. In dictyostelic types there is a broad band of wood among which a good deal of parenchyma occurs.

The xylem is surrounded by a layer of ordinary parenchyma (Vasal parenchym of Strasburger), followed by a layer of phloem cells. The phloem never consists of more than a single layer of sieve tubes, all of which are of uniform size so that there is no differentiation into protophloem and metaphloem (Text-fig. 4). The phloem does not continue around the leaf gap so that there is no continuity of internal and external phloem; surrounding the phloem are two or three layers of fairly large parenchymatous cells, which as in *Ch. tenuifolia* might be interpreted as representing a multilayered pericycle; surrounding this is the endodermis. The cells of the pericycle are of interest owing to the fact that they contain a great deal of granular matter which is always arranged at one side of the cell, and in the same direction in each cell giving the whole structure a peculiar, but distinctive, appearance. The granules lie on that side of the cell which is the lower side in the position in which the rhizome is lying. The granules are not starch granules but are evidently food granules of various kinds. This
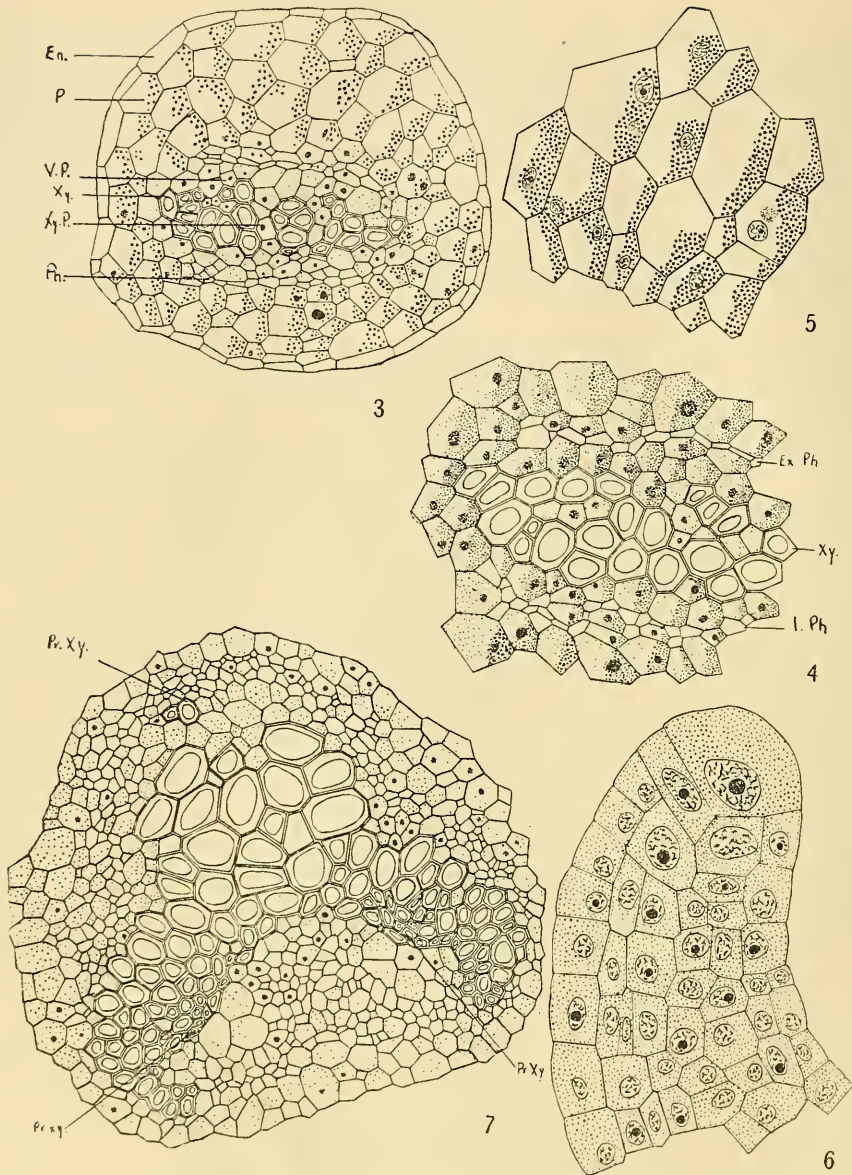
Text-fig. 3.   Transverse section of a meristele showing the central core of xylem (Xy.)
        containing xylem parenchyma (Xy.P.), surrounded by "vasal parenchym" (V.P.), a
        single layer of phloem cells (Ph.), a multilayered pericycle (P.) and the endodermis
        (En.).   × 150.
Text-fig. 4.   A portion of the above indicating the nature of the xylem (Xy.) and the
        internal (I. Ph.) and external (Ex. Ph.) phloem.   × 240.
Text-fig. 5.   A few of the cells of the pericycle indicating the position of the granules.
        × 240.
Text-fig. 6.   Longitudinal section of the apex of the leaf, indicating the two-sided wedge
        shaped apical cell and its segmentations.   × 400.
Text-fig. 7.   Transverse section of the vascular strand to the petiole.   The three
        protoxylem groups (Pr. Xy.) are shown.   × 150.

condition is not due to fixation as it is to be seen in the living material. The structure is very like that which has been described and figured by Schaefer in various root tips. The condition is evidently a purely physiological one and related to gravity. (Text-fig. 5.)

The rhizome structure at once places *Ch. vellea* as an advanced type of the genus.

B. *Leaves.*

As indicated in Text-fig. 6, the growth of the leaf is due to a two-sided, wedge shaped apical cell forming two rows of segments, such as is typical for Leptosporangiate Ferns. The outer divisions of the segments become the marginal cells of the pinnae, the other divisions produce the petiole. The young leaf invariably shows circinate vernation.
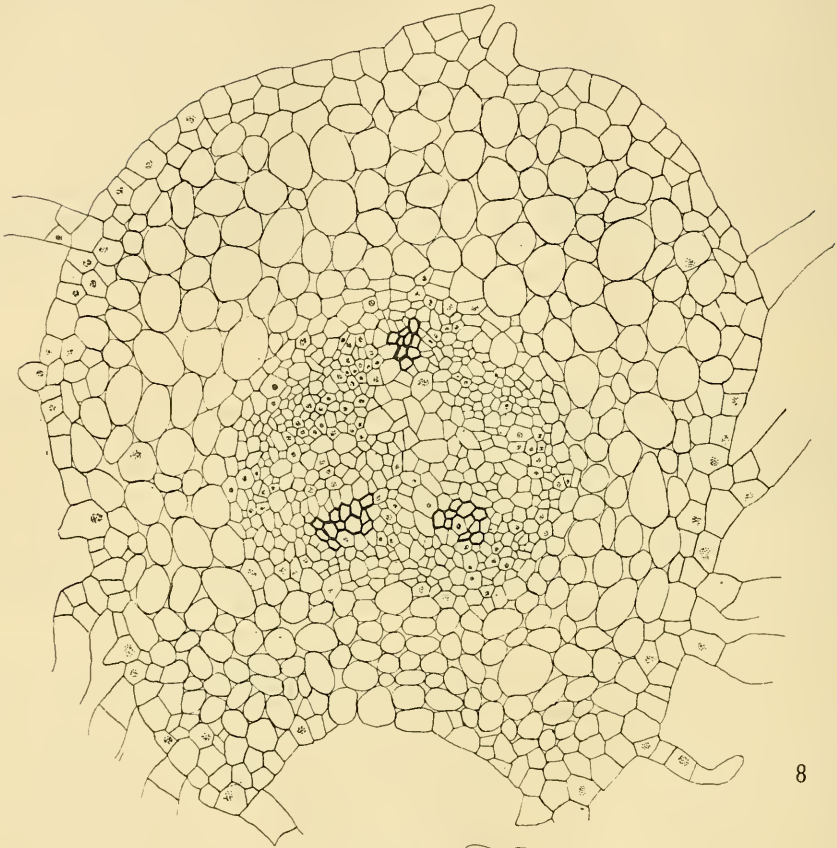
Petiole.

The petiolar stele forms a single strand surrounded by a sclerenchymatous cortex. Text-fig. 7 indicates the vascular strand, the main mass of which is composed of large metaxylem elements in conjunction with which appear three protoxylem groups. The ends of the xylem mass are slightly curved inwards. This is followed by a single layer of parenchymatous cells surrounded by a layer of phloem cells. The phloem is continuous around the strand. This is followed by a few more layers of parenchymatous cells—the pericycle—the whole being enclosed by a typical endodermis. This has usually broken down in the older parts of the petiole. The parenchymatous cells are filled with dense granular contents and contain large nuclei.

The principal interest of the petiolar stele of the genus *Cheilanthes* lies in the various positions occupied by the third median protoxylem group in the different species and at different levels of the petiole of the same species. The vascular strands of the rhizome show no visible protoxylem elements, but as soon as the leaf trace leaves the stem stele, protoxylem groups make their appearance in the trace which had hitherto been without them. As already mentioned, at the very base the condition is that of a simple adaxially curved anarch leaf trace. Text-fig. 8 indicates a section taken from the base of the young petiole. At this level there are two lateral, endarch protoxylem groups, while the third median group is distinctly exarch in position and attached to the as yet unlignified metaxylem elements.

Text-figs. 7 and 9 indicate sections made at higher levels of the petiole. Here the median protoxylem group has become completely detached from the metaxylem and is separated from it by parenchyma. The number of tracheids composing this group is also very much less usually consisting of two or three tracheids often widely separated. At higher levels this group dies out altogether.

The condition here described can easily be brought into line with that which occurs in the species described by Marsh (1914) and that of *Ch. tenuifolia* (Williams, 1924).

Marsh (1914, p. 678) maintains that in all the species which he investigated there was at the base a simple adaxially curved anarch leaf trace, but as the petiolar strand is followed upwards changes occur in the petiolar strand which vary considerably. These changes may be briefly outlined as follows: In *Ch. fendleri* the anarch strand soon develops three protoxylems all of which are endarch. The metaxylem immediately exterior to the median protoxylem group dies out;

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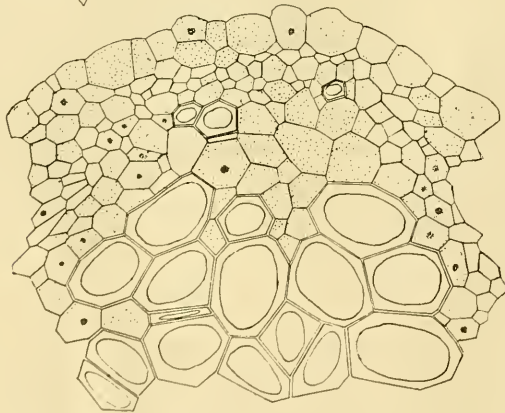
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Text-fig. 8. Transverse section of the young petiole near the base. The relative positions of the three protoxylem groups are clear. × 150.

Text-fig. 9. Transverse section of the upper portion of the petiolar stele at a higher level. The median protoxylem group is here detached and broken up. × 240.

the two portions of the stele soon rejoin, but the junction is effected in such a way that the protoxylem is now exarch in position. The protoxylem next becomes completely detached and runs through the major portion of the petiole as a single separate group. Later it becomes broken into three or four smaller groups.

In *Ch. lanuginosa* the three protoxylem groups appear at the base, but at this point the centre of the trace is so narrow that the median protoxylem occupies the whole of the thickness of the stele. The two metaxylem masses rejoin, but the median protoxylem does not persist. It is found for a short distance as a line of thickening among the parenchyma but at higher levels no trace of it can be recognized.

In *Ch. gracillima* the two lateral protoxylems occupying an endarch position are the only ones which can ever be definitely recognized at any level of the petiole.

In *Ch. persica* the petiolar stele has the shape of an obtuse angled isosceles triangle, and has the three protoxylem groups at each angle.

In *Ch. tenuifolia* (Williams, 1924, p. 384-385) the petiolar stele is described as consisting of, at the base, a simple adaxially curved anarch structure. When the protoxylem groups appear, the two lateral components take up the typical endarch position, while the metaxylem immediately exterior to the median protoxylem has died out, leaving the protoxylem as the sole junction between these two masses. These, however, soon rejoin, and median protoxylem becomes exarch. At a higher level it was found to be detached from the metaxylem elements.

It is thus seen that *Ch. tenuifolia* might be interpreted as a form intermediate between *Ch. fendleri* and *Ch. lanuginosa* with regard to the structure of the petiolar stele, since various stages at the base of the petiole in *Ch. fendleri* are not present in *Ch. tenuifolia*, while various phases at the apex in *Ch. lanuginosa* are not represented in *Ch. tenuifolia*. In the same manner *Ch. vellea* might be described as intermediate between *Ch. lanuginosa* and *Ch. gracillima* for the type of petiolar structure.

Marsh (1914, p. 680) maintains that these facts admit of but one explanation, that is, that the base of the leaf preserves primitive characters. He considers that it is difficult to imagine what could actually be the cause of the exarchy and detachment of the median protoxylem: it is simple from a study of leaf base transition to derive *Ch. fendleri* from the normal type and the *Cheilanthes* petioles from *Ch. fendleri*. He also states (p. 681) that in deriving *Ch. lanuginosa* and *Ch. gracillima* from *Ch. fendleri* that the earlier stages may be dropped out at the base of the petiole. This dropping out of the earlier stages is also to be observed in *Ch. vellea* and *Ch. tenuifolia*.

Sinnot (1911) maintains that in the triarch petiolar stele, it is always the median protoxylem group which more readily becomes broken up into two groups. He has also spoken of the "striking constancy" of endarchy in the filicinean petiolar stele. The investigations recorded on the various species of *Cheilanthes* illustrate very well the plasticity of the median group with its gradual movement from an endarch to an exarch position and finally its complete separation and disintegration. While these types mainly agree with Sinnot's generalizations of the filicinean leaf trace, they certainly do seem to have slipped ahead in the general evolutionary scheme.

It is quite generally recognized that the stem and petiolar structure are simply and fundamentally the result of an adaptation to the demands made upon
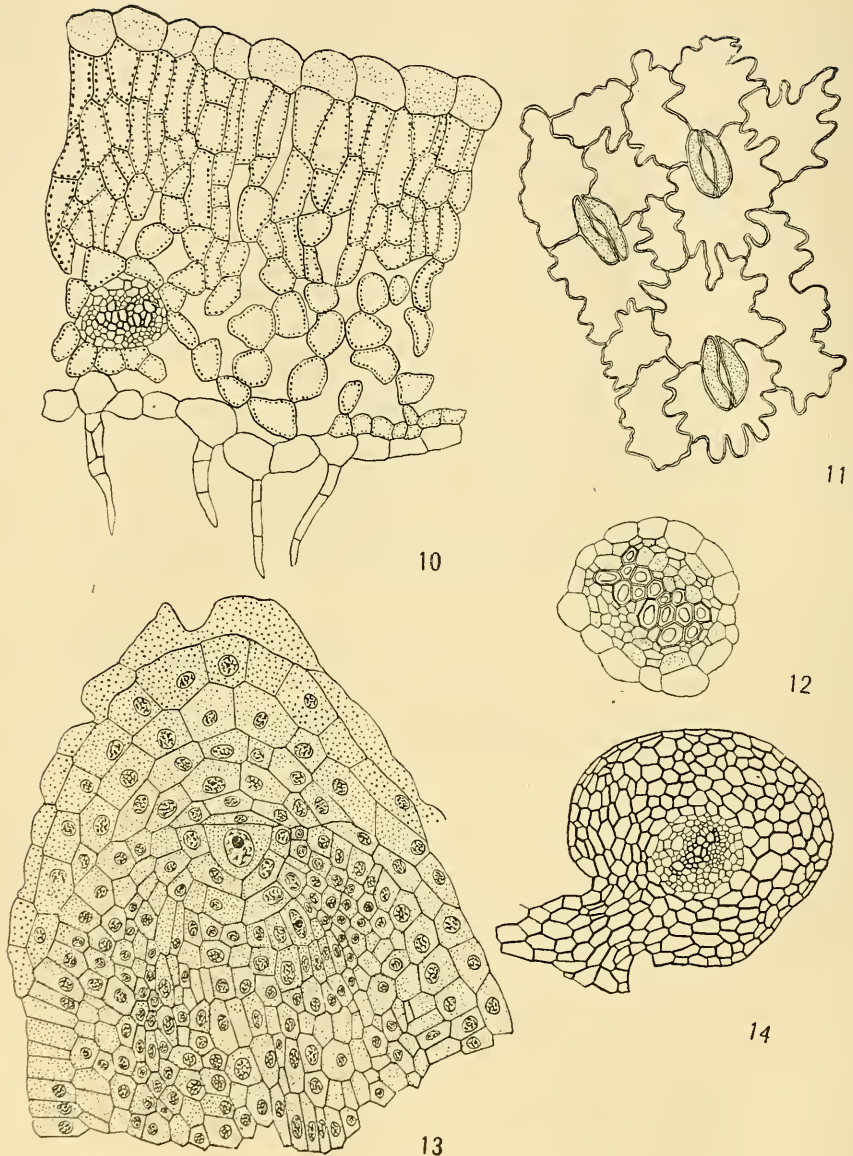
Text-fig. 10.   Transverse section of the pinnule indicating the nature of the upper and
        lower epidermis, the palisade and lacunar tissue.   × 150.

Text-fig. 11.   A surface section of the lower surface of the pinnule, indicating the nature
        of the stomata.   × 150.

Text-fig. 12.   Transverse section of the vascular bundle of the pinnule.   × 240.

Text-fig. 13.   Transverse section of the apex of the root showing the apical cell with its
        typical segmentation.   × 240.

Text-fig. 14.   Transverse section of the root showing the sclerized cortex and the central
        vascular strand.   × 60.

these parts by the foliage. Taking this fact into consideration, it might be well to look to the habitat of these Ferns for explanations of any peculiar types of structure present in the stem or petiole. It will be remembered that these ferns are typically xerophytic. Other small ferns found growing under similar xerophytic conditions are *Lindsaya linearis* and *L. microphylla*. The writer has investigated the anatomy of these types (1925) and observed in the petiolar steles the same exarch positions of the median protoxylem groups. In these types, however, there was not to be observed that transition from an endarch to an exarch position.

The tentative explanation offered for this variation in the position of the median group is that it is a response to the unique habitat of these ferns; that is, it is an adaptation to dry conditions.

Pinnule.

The pinnules are lobed; the veins show dichotomous venation, and on the ends of these forked veins the sori are borne. The lower surface of the leaf is protected by a dense mass of hairs.

Text-fig. 10 indicates the minute anatomy of the pinnule. This is very similar to that of *Ch. tenuifolia*. The cells of the upper epidermis are large, are filled with dense granular contents, and are protected by the cuticle. The lower epidermis consists of relatively thin walled cells, and from these grow out the dense mass of hairs which cover the lower surface. The stomata are confined to the lower epidermis and open into large air cavities; they are protected by the inrolled margins of the pinnule plus a covering of hairs. (Text-fig. 11.)

The lacunar tissue is reduced, while the palisade tissue is well developed, often being three cell layers deep. The cells are oblong in shape, and the chloroplasts are arranged, for the most part, along the margins of their walls (Text-fig. 10). The vascular bundles of the pinnae are usually collateral. Each is surrounded by a well defined endodermis, the cells being large, colourless and thin walled. This encloses a layer of parenchymatous cells—the pericycle—which surrounds a central mass of xylem tracheids and a few sieve tubes representing the phloem (Text-fig. 12).

A vascular commissure carries the vascular supplies to the developing sporangia.

From these remarks, it will be seen that the leaf, both in external morphology and minute anatomy, shows well marked adaptations to its xerophilous habitat.

C. *Root.*

The roots present no features of particular importance in the present discussion. They arise in connection with the bases of the leaves. The primary roots branch profusely; the secondary roots are produced in two lines corresponding to the protoxylem groups in the vascular bundle of the primary root.

The apex is characterized by the presence of a three sided, pyramidal apical cell, from which segments are cut off in the usual manner (Text-fig. 13).

Text-fig. 14 indicates the minute anatomy of the older root. Here the cortex has become sclerized and surrounds a diarch vascular strand. The latter is composed of a central core of xylem, the metaxylem elements being large and few with the protoxylem groups arranged at the ends. The phloem consists of a single row of sieve tubes which do not continue around the protoxylem groups. The xylem and phloem are separated by one or two layers of parenchyma. Surrounding the phloem and separating it from the endodermis, are three or four

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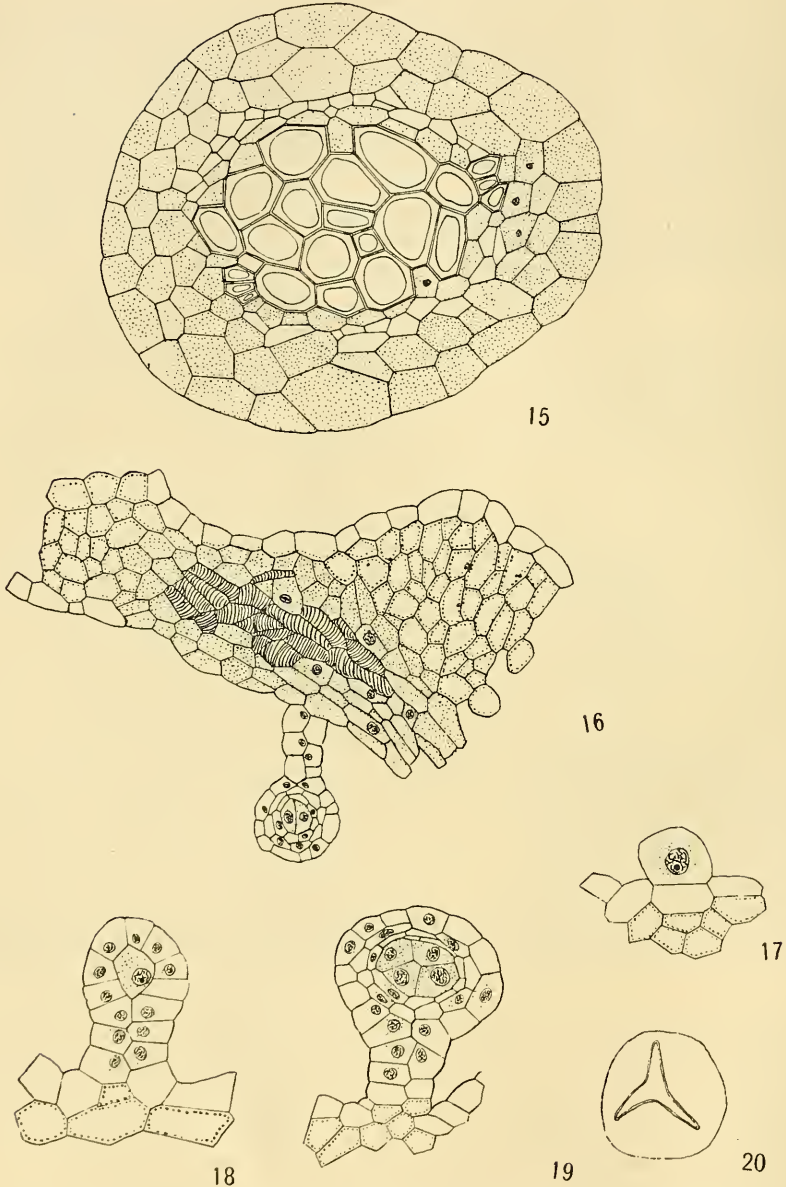
Text-fig. 15.   Transverse section of the vascular bundle of the root, indicating its diarch nature.   × 240.

Text-fig. 16.   This indicates the nature of the soral region of the pinnule.   × 150.

Text-fig. 17.   This indicates the nature of the first segmentation occurring in the sporangium.   × 240.

Text-fig. 18.   This indicates that stage in the development of the sporangium when the wall and stalk cells are formed and the central cell which will form the archeosporium proper.   × 240.

Text-fig. 19.   The typical quadrant stage of development of the sporangium.   × 240.

Text-fig. 20.   This indicates the nature of the mature spore.   × 240.

layers of parenchymatous cells which might be interpreted as representing the pericycle. The parenchymatous cells have dense granular contents and large nuclei (Text-fig. 15).

D. *Sorus.*

The sori are superficial and continuous on the back of unthickened nerve endings. They are protected by a false indusium which is composed of the inrolled margin of the pinnule. The soral region is represented in Text-fig. 16. It is broad and flat and shows the typical mixed character with regard to the arrangement of the sporangia.

The development of the sporangia is identical with that described in *Ch. tenuifolia* (Williams, 1924), hence for that typical for Leptosporangiate Ferns. The sporangia arise from an epidermal cell which protrudes above the surface and becomes divided by a transverse wall into a base or stalk cell and an upper cell which forms the sporangium proper. Since development is of the general nature typical for Leptosporangiate Ferns, there is no need to describe it here. Various stages in the development are represented in Text-figs. 17, 18, 19.

The annulus is vertical and interrupted by the stalk. The number of spores produced in each sporangium does not exceed 16-20. The nature of the mature spore is shown in Text-fig. 20.

Conclusions.

The convergence of evidence seems to indicate that the genus *Cheilanthes* represents a group of ferns which in the earlier types show anatomically primitive characters, but possessing soral characters which are advanced. In some species, the stem stele becomes more complicated by the insertion of extra leaves and the overlapping of the gaps formed by their departure. These primitive anatomical characters present in the stem might perhaps be interpreted in terms of the habitat of these ferns, combined with the reduction in the foliage.

In all parts of these ferns there are striking adaptations to xerophily. Marsh (1914, p. 677) regards the reduction in the number of sieve tubes constituting the phloem in all parts of the plants as such an adaptation. He states that "the phloem of these forms is remarkable for the absence of differentiation into protophloem and metaphloem. . . The whole of the phloem of these forms may fairly be said to correspond with the protophloem of mesophytic species, the slow growth, necessitated by the xerophilous habitat rendering unnecessary those facilities for active translocation which would be given by large metaphloem elements." The writer has also suggested that the structure of the petiole with the peculiar movement of the median protoxylem group is of the nature of a response to the unique environment of these ferns.

Summary.

1. The apex of the stem is occupied by a tetrahedral apical cell cutting off segments parallel to the cutting faces.

2. The stem stele is of that type of anatomy known as the dictyostele; this at once places *Ch. vellea* as one of the more advanced species belonging to the genus.

3. The leaf is formed by segmentation from a two-sided, wedge shaped apical cell.

4. The petiolar stele as it leaves the stem stele is a simple adaxially curved anarch leaf trace.

5. When the protoxylem groups appear, the two lateral components are endarch in position while the median group is exarch.

6. At higher levels in the petiole the median protoxylem group becomes detached from the metaxylem elements; it becomes broken into three or four smaller groups and finally disappears.

7. The pinnae have a reduced lacunar system and a well developed palisade.

8. The stomata are confined to the lower surface of the pinnae and are protected by the inrolled margins of the pinnae together with a covering of hairs.

9. The vascular bundles of the pinnae are collateral.

10. The apex of the root is occupied by a three sided apical cell with typical segmentations.

11. The root is diarch.

12. The sorus is superficial in origin and continuous. It is protected by the inrolled margins of the leaf alone.

13. The development of the sporangia conforms with that typical for Leptosporangiate Ferns.

14. *Cheilanthes vellea* shows, both in external morphology and internal anatomy, well marked adaptations to its xerophilous habitat.

In conclusion, the writer wishes to express her thanks to Professor Lawson, in whose laboratory the investigation was carried out, for advice and guidance.

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